

Basic Questions of Systematics

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THE following discussion is based on the introduction to my monograph on the neotropical army ants (1955). As is well known, revisionary studies not only broaden our factual knowledge, but also permit an amazing insight into the nature of systematic research, about which the most contradictory views are in circulation.

Systematics as a Science

Systematics or taxonomy can be defined as that branch of biological science which explores the order existing in the Plant and Animal Kingdoms and represents it by means of a system of concepts (the categories). That there is order in nature is a presupposition of any scientific research, as Caldin exhaustively demonstrated in his book *The Power and Limits of Science* (1949, p. 61). Nature is not a Chaos but a Cosmos. There is a system in nature, independent of any human consideration. The systematist seeks to reproduce this system of nature in a natural system. Order is not carried into nature, but rather it is abstracted from her. "Nature itself has her own system with regard to which the systems of the authors are only successive approximations" (Agassiz, 1869, p. 51).

As the science of order ("taxonomy"), systematics is a pure science of relations, unconcerned with time, space, or cause. Unconcerned with *time*: systematics is non-historic and essentially static; it knows only a simple juxtaposition of different conditions of form. Unconcerned with *space*: geographical factors are not primary criteria in the definition of taxonomic units. Unconcerned with *cause*: systematics has no explanatory function as far as the origin of the system is concerned; it is merely comparing, determining, and classifying. "Systematics is only

directed to an apprehension and orderly arrangement of the stable elements in nature, which exist as actual facts independent of any theory or interpretation. . . . It seeks to express the order and relationships existing in the objects themselves, but does not say anything about their origin." (Schindewolf, 1950, p. 436, trans.) "Any kind of systematics is independent of the possible origin of the objects to be classified" (Kuhn, 1951, p. 155, trans.). Horn stated: "Taxonomy is ordering, without saying anything about the way in which this order has come into being." (1929a, p. 42.)

Systematics is a true science, because science is nothing more than demonstrable knowledge, rationalized perception. Its method is inductive, like that of all natural science. It rests on observation and intellectual penetration, on analysis and synthesis. *All* facts observed which can help the systematist to build the system are important to him. This includes even the genetic relations of the organisms, for example, the facts of sexual dimorphism and polymorphism observed in the army-ant genus *Eciton*. But the real task of the systematist begins only then, and it consists in morphological comparison; so that in the case of *Eciton*, we can talk about worker-systematics, female-systematics, and male-systematics. The systematist is therefore a biologist and a comparative morphologist at the same time. Even Linnaeus was not a mere cataloguer or "skin-zoologist" concerned only with external characters, as we read many times. If he had known all the castes of *Dorylus helvolus*, he would certainly not have described the species as *Vespa* nor would he have named separately each of the three castes.

Comparative morphology is the backbone of systematic research. Form stands

at the center of interest. The phenotypic characters observed and the conditions of similarity are not counted; they are rather, as it were, evaluated (cf. Remane, 1952, pp. 6-11). Differences in form cannot be mathematically conceived. Systematics has nothing to do with "mathematical logic" (cf. Horn, 1933, p. 132; Hennig, 1950, p. 150). Rensch (1934, p. 110) wants to extend Kant's statement that there is as much of real science in any science as there is of mathematics, to the field of taxonomy; this view must be decisively rejected. I know of no systematist exclusively preoccupied with the quantitative analysis of characters. "The mathematical machine works with unerring precision; but what we get out of it is nothing more than a rearrangement of what we put into it" (Thompson, 1937, p. 114).

The inductive method works perfectly in the field of the so-called "exact" sciences, for instance in physics. The exact sciences state their laws in quantitative form; they are necessarily mathematical. Zoology is not an exact science in this sense, but its true results are certain and absolutely binding. However, it frequently takes a long time to achieve a system that represents the true reality of nature. For instance, let us take the story of the army-ant *Eciton burchelli*: The male was described in 1842 as *Labidus* by Westwood; the soldier was made known by Mayr in 1886 under the name of *Eciton foreli*; and the female was first discovered by Wheeler in 1921. In his work the systematist for the most part has only fragments of nature on hand, therefore his results are often only an approximation to reality. "Science commonly advances by successive improvements of approximate statements" (Caldin, p. 66). Nature is highly complex and the multiplicity of forms is oppressive. Moreover, there is the subjective element which is present in any observation and evaluation of morphological relationships; this subjective element has a disturbing effect on the certainty of taxonomic concepts. The present state of research in certain groups of insects re-

sembles chaos rather than a system. But the working method of systematics is essentially sound and is likely to deliver definite results, provided that it is properly handled.

Systematics has been contemptuously designated as only cataloguing or "pigeonholing" of specimens. Whoever thinks this, has no idea of the essence of systematic research. Just as it would not occur to a chemist to compare the study of the system of elements with the cataloguing of a librarian, and just as the discovery of a new chemical element is rightly celebrated as a scientific feat, so the investigation and classification of the elementary units of the zoological system, *i.e.*, the species, constitute a scientific study which has nothing to do with simple recording. Discovery, designation, and diagnosis of an actual new species which exists in nature as a biological unit, is equivalent to discovery of a new chemical element. It is a step forward into the *terra incognita* of nature, it is the erection of a new systematic concept which demands general recognition. For example, no sophistry can ever banish the concept *Eciton burchelli* from the annals of science. The populations corresponding to this concept may die out; but the concept remains. "Extinct species have not ceased being species, even though none still live" (de Laubenfels, 1953, p. 44).

Systematics and Phylogeny

Systematics is independent of the theory of descent. This is admitted today even by convinced evolutionists. The reasons are as follows. (1) Systematic methods provide definite results without reference to the idea of evolution; phylogenetics has no special methods, it is essentially the interpretation of systematic facts. (2) Systematics is a science; phylogeny is a hypothesis of a historical process containing a fundamentally unverifiable element (Thompson) and can therefore never be the foundation of a science. (3) Systematics is investigation of facts;

phylogenetics is often "a dangerous play with mere possibilities" (Hennig); Kant called it "a daring adventure of the mind."

Of course, any systematist is free to speculate on the probable phylogeny of certain species or genera, on the basis of systematic facts. In my "Studies of *Atta*" (1950), I myself tried to reconstruct the probable evolution of this genus, proceeding from the geographical distribution of the species and the structure of the male genitalia. But such theoretical considerations can only be evaluated as a supplement to systematics; they are without effect on true systematic research.

The widely held view that systematics must be based on phylogeny, and that to be natural the system must be a phylogenetic one, is nothing more than a relic of Darwinism. Exactly the reverse is true: phylogenetics is for the most part based on the facts of systematics. There is, therefore, no "phylogenetic systematics" but rather, as Naef has already emphasized, only a phylogenetic interpretation of systematic facts. Phylogenetics is nothing more than a "theoretical supplement to natural systematics" (Naef, 1933, p. 38). The botanist Allan wrote (1940, p. 515):

The view that taxonomy should be based on phylogeny is very popular and is *ex cathedra* imposing. But the argument is too apt to be circular, and the 'phylogenetic' charts are generally based on taxonomic findings into which we read phylogeny, rather than deduced from any true knowledge of descent. Our phylogenies are invented to account for our taxonomic facts or theories.

And the paleontologist Schindewolf expressed himself as follows (1950, p. 461):

Morphology and its precipitation into the natural system form the basis for the general theory of descent and the special history of evolution, but phylogeny is by no means the foundation of the system. The phylogenetic consideration only *secondarily* carries a historico-genetic, dynamic momentum into the system that already statically exists according to form and content, and tries to interpret the conceptual form-relationship as the expression of an actual blood-relationship. That is absolutely justified and even necessary, unless we are willing to relinquish an understanding of the forms. But it should be kept in mind that

this is only an *interpretation of the existing system* and that no new insights have been obtained by a special phylogenetic method. [Translation.]

Walther Horn expressed similar thoughts at the Third Convention of German Entomologists in Giessen (1929d):

Zoology is a science and phylogeny is a matter of belief. In our systematic studies of Recent and sub-Recent insects it is of relatively little consequence whether we are monophyleticists, polyphyleticists, or aphyleticists. The main thing is whether we recognize and make use of the systematic relationships. From the aphyletic attitude there can never result any detriment to systematic work. Its aim is simple typological biology, exactly as in the old comparative anatomy and the modern comparative physiology. [Translation.]

That very valuable systematic work can be accomplished with the aphyletic attitude is evident from the generic revision of Cynipoidea by Lewis H. Weld (1952), of which the author remarked right at the beginning: "This is not a contribution to the literature of evolution." I have worked with this difficult group myself and am persuaded that Weld's paper will be basic for a long time. If Kinsey's papers (1930, 1936) are compared with it, the following statement of Horn will be recalled (1929d, p. 93, trans.): "Theoretically, phylogeny is a beautiful idea, but it is often harmful by reason of the fact that on the basis of prejudiced, one-sided, and therefore insufficient preliminary studies it leads to the drawing of fantastic conclusions which seem to be well-founded, whereas in reality they only *conceal a defective systematic work*." Or, as a friend of mine put it: "Phylogeny is usually an attempt to hide poor taxonomy under a flowery mantle of respectability." Weld is a comparative morphologist; Kinsey a phylogenetic visionary. I cannot confirm the idea that his monographs have led to "basic general knowledge" as Sachtleben (1937) thought in a review. But that he had no clear systematic concepts and thereby caused great confusion, is clearly evident from Weld's work.

I shall conclude this section with the following citation from a paper by Blackwelder and Boyden (1952, p. 31):

The grand object of classification everywhere is the same. It is to group the objects of study in accordance with their essential natures. . . . But in biology, since Darwin's *Origin of Species* appeared, biologists have substituted for this grand object that of "expressing the phylogenetic relationships" of organisms, a substitution which has introduced endless confusion into taxonomic theory and practice.

Systematics and Genetics

Systematics and genetics are two basically different disciplines of biology. Each has its own methods and its own problems. Systematics asks, "What is?"; genetics, "What will be?" Systematics works with morphological comparison, genetics with experiment. Systematics creates general concepts for constant entities; genetics makes causal analyses of modifications. Since there is only one truth, the definite results of the two sciences cannot contradict, rather they can at most complement each other.

The systematist is convinced that differences in the genotype are accompanied by visible differences in the phenotype, and that exact analysis of these differences is a positive way of expressing the multiplicity of organic forms in a system of categories. "After all, systematics cannot erect a nomenclature on the basis of genes and chromosomes. Concepts like 'dominant', 'recessive', etc., cannot be simply transferred to systematics; 'homozygote' and 'species' are two different things! Populations play an entirely different role in systematics than in genetics." (Horn, 1933, pp. 136-137, trans.)

One of the greatest dangers threatening systematics is the effort of certain geneticists to demolish the concept of species. They speak of pure lines, elementary species, biotypes, microraces, etc., and try to force the Linnean species out of its central position, so that one geneticist, the famous Johannsen, has even published the harsh opinion that the species concept, on ac-

count of its arbitrary interpretation, is only comparable to the concept of sausage, lettuce, and ink! (Horn, 1933, p. 134). The botanist Allan says (1940, p. 315): "The searching analyses of the geneticists begin to assume impressive proportions, but have revealed a great danger. Important and necessary as the delimitation of microspecies may be, we must hold fast to the broader concept of species if we are not to miss the forest by getting lost among the trees." Recently, the famous Swedish geneticist Heribert Nilsson took an energetic position against the species splitters and excessive species makers in his important work *Synthetische Artbildung* (1953).

The problem of the origin of species has not been experimentally resolved despite assertions to the contrary. Woltereck (1931, p. 300) assured

that experimental genetics . . . did not advance beyond the pleomorphy of races and replaceable characters and it must make a halt before the problem of species formation and species descent as before a smooth wall, in spite of successes and results hitherto unheard of in biology. . . . What kind of wall is this which is raised between the results of our experiments and the problem which is supposed to be finally explained by those experiments? We seek for the mechanism of *speciation*, and find always again and in always clearer light, the phenomenon of *variation*. Why are these variants of no decisive use to us in understanding speciation? . . . Because the species are not increased and diversified variants, as we have hitherto assumed, but they are biological entities and stable elements in nature which belong to a category essentially different from that of the variants. Just as we are not able to produce a single gene-modification by way of the accumulation and intensification of phenotypical differences, we seem also incapable to produce a new constitution, a new species, a new type at any time by the increase and accumulation of additive racial characters. [Translation.]

The Nature of Systematic Categories

All systematic categories (phylum, class, order, family, genus, species) are universal concepts abstracted from the individuals. As concepts, they exist only in the mind, but we find the basis for these

concepts in nature. As the old logicians said, they are "*entia rationis cum fundamento in re*." The categories are, therefore, not concrete things, as Nägeli and Heincke asserted. No more are they purely subjective fictions with no basis in reality as others (Zimmermann, Mertens, Dürken) think. Nor is it correct to say with Mayr that the "species" are realities, but the higher categories are pure abstractions. "Only the individuals have true reality, tangible objectivity, which can be perceived by the senses. But a single individual never represents the whole species concept." (Schindewolf, 1950, p. 437, in translation.)

The nature of categories can easily be made clear if we begin with the artifacts of human workmanship. General concepts such as "chair," "table," "cupboard" are immediately comprehensible in daily life. When I speak of "chair," I do not mean this or that individual chair, but rather what is common to all chairs, the concept "chair." This concept is not an arbitrary fiction. No more is it something real in the sense that individuals are real. It is simply a general concept or an abstraction "with a basis in reality." The same applies to the group-concept "furniture," by which I can put together the "species"-concepts of "chair," "table," and "cupboard."

In nature too, there are "group-formations of different rank and extent, and those are *objective facts* which are the foundations of our categories no matter what designations they have" (Schindewolf, 1950, p. 441, trans.). The systematist can, therefore, not act purely arbitrarily like the astronomer who combines several stars in a constellation. The systematist must keep to the similarities and differences present in organisms. A few systematists may be idealists in theory, but all of them are realists in practice. The realistic-minded systematist is convinced that the essential orderliness of nature can be laid bare and can be expressed by concepts which are meant to apply, as the old logicians said "*toti et soli definito*."

Let us take the group-concept "ant." It is unimportant whether we call it "Formicidae" or "Formicoidea;" that is, whether we evaluate the group as a family or a superfamily. It is important only that this group-concept is founded in nature. Delimitation of this concept is not a matter of agreement or convenience. The extent of this concept is permanent and stable. The concept was derived from observation of nature. It would be absurd to call such an objectively well-founded concept a fiction of the human mind. What is understood by "ant" has been established for all time.—It is not to be denied that arbitrary concepts do exist in zoological nomenclature. But then, the systematist is arbitrary, not nature. In nature there is order, in nomenclature unfortunately we often find chaos.

What applies to the concept "family," also applies to the concept "genus." It is an abstraction "with a foundation in reality." Therefore it is by no means a purely subjective fiction or an "artificial creation" (Mayr, 1949, p. 491) but a natural unit. Whether a genus is large or small, whether it includes many or only a few species does not finally depend on the subjective judgment of the taxonomist. Independent of any phylogenetic speculation, the systematist must try to recognize and define unequivocally the generic groups by careful morphological comparison of species. A thousand-fold experience demonstrates the fact that there are generic groupings in nature which are separated from each other by sharp gaps. The delimitation of genera may be subject to fluctuations which depend partly upon the experience of the taxonomist, partly also on the degree of knowledge to which research has advanced in a certain group. "Concepts of genera change with the increased knowledge of individual species" (Weld, 1952, p. 345). But barriers are set up against subjective evaluation of generic characters by the facts existing in nature. These fluctuations will certainly come to a standstill when all the facts are known and have been objectively evaluated. If

this goal of a rational penetration of reality, which is the ideal in the mind of the systematist, were not attainable, no systematics would have any sense at all. Without this belief the incredible labors of taxonomists would be without hope. The difficulty of the task forms the stimulus and the motivation of systematic research.

What the investigator finds in nature is a graduated multiplicity of forms. This makes possible the erection of an hierarchic system consisting of a series of categories. These are in a definite condition of subordination. The higher categories include those of lower rank down to species. Every category represents an idea or a type, but this idea is based on facts, provided that it was "naturally" and not "artificially" formed. The systematist is therefore an idealist and a realist at the same time. Comparative morphology is both "idealistic" morphology and empirical research. But all research begins with the individual. The pure idea of form, the pure type, exists nowhere in nature. For instance, there are no ants which would present only the general characters of the family Formicidae. But

every individual embodies the complex of characters . . . of the sum-total of hierarchic types to which it belongs. It therefore simultaneously embodies the type of its species, its genus, family, order, etc., and it is a matter of comparative and abstractive consideration to sift these type characters of varying size and extent, and to separate them from each other. [Schindewolf, 1950, p. 241, trans.]

The Species as Fundamental Unit of the System

The concept of species as "the group of individuals distinguished by an irreducible set of constant properties and connected by descent and genetic relationship" (Thompson, 1937, p. 24) forms the real fundamental unit of the system. Every animal unequivocally belongs to a certain species. All organic nature is specifically constituted; this applies both to recent and to fossil organisms. This fact

is supported by so overwhelming a number of observations that it must be designated a natural law. It is also granted by convinced evolutionists.

The geneticist Bateson wrote (1894, p. 2): "The existence of specific differences is one of the characteristics of the forms of living things. This is no merely subjective conception but an objective, tangible fact So much is being said of the mutability of species that this which is *the central fact of Natural History* is almost lost sight of, but . . . this fact must be boldly faced. There is nothing to be gained by shirking or trying to forget it." Twenty years later (1913, p. 12) he expressed the same thoughts: "Specificity is a universal attribute of organized life."

Another geneticist, Dobzhansky, writes (1937, p. 306): "There is a single systematic category which, in contrast to others, withstood all the changes in the nomenclature with an amazing tenacity. That is the category of species In most animal and plant groups, except in the so-called difficult ones, the delimitation of species is subject to no dispute." And again (p. 309): "Despite all the difficulties encountered in classifying species in certain exceptional groups of organisms, biologists have continued to feel that there is something about species that makes them more definite entities than all other categories."

At the 87th Meeting of the Society of German Naturalists in Leipzig in 1922, the paleontologist Johannes Walther made the following declaration which caused no little excitement (1923, p. 153):

When I concluded my biological training in Jena 40 years ago, in order to devote myself entirely to the study of ancient life and its geological environment, I approached the factual material with the principles which my teacher Ernst Haeckel had so spiritedly supported to the last. Fascinated by his ideas, it seemed to me an easy and successful task to follow up the series of forms gliding slowly from one to another and to prove their causal dependence on the changes in environment. But during my work I was gradually forced to give up that suggestive point of view, and with time I became firmly convinced *that the*

species were just as constant in past ages as they are at present. Just as today there are some species which vary greatly and live among numerous "good" species which do not vary at all, so has it always been. There have been greatly varying forms in every geological period, but they are just as extinct as their companions which did not mutate, and no causal historical connection whatever can be discovered between variation and species formation in the geological periods that are past. [Translation.]

Since Darwin's "Origin of Species" (1859) there has been a tendency among biologists to doubt the fundamental importance of the species and to deny its central position. The species are considered as increased varieties, but it has been forgotten that the concept "variation" has no meaning and is without content unless the specific definition has been clearly established before. Therefore Agassiz has already asked: "If there are no species, how can they vary?" And Bateson says (1893, p. 80): "The belief that living beings are plastic conglomerates of miscellaneous attributes . . . is a fancy which the study of variation does not support." In his recent work *Synthetische Artbildung* (1953, p. 252) Nilsson writes (in translation): "To Darwin evolution was a gradual problem . . . Everything was in a continuous flux. Thus it was easy to get over the species limits. But here is the fundamental difficulty according to our experience with the structure of the species. It is unsurmountable. For the species is not made up of pan-genes which can be displaced, but rather it is composed of hereditary genes which are stable . . . The species is constant."

What the conscientious systematist who is aware of his responsibilities discovers in nature, is not a planless flux of indefinitely plastic forms, but rather separate species which can be distinguished by a certain set of common characteristics. "Even the presence of more or less numerous mutations, races, subspecies, and the like, within the species does not alter the fact that the fluent transitions demanded by continual change are not forthcoming. The world of living and fossil organisms

is not a continuum but a discontinuum" (Bertalanffy, 1949, p. 95). All species, both the monotypic and the polytypic ones, are separated from each other by sharp gaps. "It is an uncontestable fact that all species of animals and plants are separated from each other by absolute and clear-cut characters" (Godron, 1873, p. 372). Therefore, Woltereck (1931, p. 280, trans.) claims: "The old concept of the true species as a biological entity, which almost became dissolved into elementary species, biotypes, etc., must again take up the central position which it has always occupied in the mind of systematists and specialists."

Mayr (1949, p. 103) says: "It is a curious paradox that so many taxonomists still adhere to a strictly static species concept, even though they admit freely the existence of evolution." To that it can be replied that the static species concept is forced upon the systematist by the facts. We can speak of "dynamic" species only in the sense that certain species produce races or subspecies, but the formation of races is rigidly bound to the species limits and every *Rassenkreis* is only a pleomorphic species which is sharply separated from every other species. That is admitted by Mayr himself when he says of Kleinschmidt and Goldschmidt (p. 114): "They claim that all evidence for intergradation between species which was quoted in the past was actually based on cases of infraspecific variation and, in all honesty, it must be admitted that this claim is largely justified."

In the case of the polytypic species of *Eciton*, for instance *mexicanum*, *burchelli* and *vagans*, the specific characters in the vast area of distribution from Argentina to Mexico are absolutely constant and every individual (whether worker, female, or male) of any race of these three species out of the whole range leaves no doubt of any kind as to which of the said species it belongs. This stability is still more surprising in the world-wide distribution of some monotypic species, i.e., of species which do not form races. In the

case of the polytropical phorid flies *Dip-loneura cornuta* and *Megaselia scalaris*, for instance, specimens from different continents are practically identical. The same applies to *Musca domestica*. Allan had the same experience with plants (1940, p. 515): "*Capsella bursa-pastoris* Medic. travels the world over, may drop certain forms here and there, but does not change into something else." Schilder nevertheless in his *Einführung in die Biotaxonomie* (1952, p. 21) remarks (in translation): "One must be sceptical of all statements on 'world-wide' distribution of homogeneous forms. . . ." We know whence this scepticism comes: It comes from the preconceived opinion that all species with a wide geographic distribution *must* form races. The tendency to do violence to facts in order to save an idea is clearly apparent.

It has been asserted again and again that a generally valid definition of "species" has not yet been found. I hold that to be an error. There is a whole series of good definitions which take both the genetic and the morphological element into consideration. One of the best is that given by Cuvier (1829); one of the worst that of the phylogeneticist Zimmermann (1948, p. 194). The last runs as follows (in translation): "Groups of organisms which are so similar that on superficial observation they are considered to be 'of the same kind,' that is, that they can be confused, or that a large concordance of hereditary structure can be assumed." The same author considers it "a matter of convenience where the lines between species are drawn." Also according to Dürken (1924, p. 46, trans.) "the species concept is carried into nature by man. . . . There are no natural species limits." Contrary to that, on the basis of my taxonomic experience, I hold fast to the opinion that the species is a natural phenomenon and a biological unit based on objective facts. Let us take, for example, the species of *Eciton* for which all the castes are known and which can therefore be considered as clarified. There can be

no doubt about their specific difference. The concepts which the systematist combines with *Eciton burchelli*, *quadriglume*, *dulcius*, *vagans*, *mexicanum*, *hamatum*, are fixed for all time and are absolutely binding. Arbitrary concepts can never compel general recognition. Meglitsch says rightly (1954, p. 53): "The systematist may be arbitrary, the species is not."

The "biological" species concept is not an invention of the "New Systematics." There has never been any other species concept than the biological one. Even Linnaeus knew and used it. Cuvier, a representative of "Linnaeism" defined the species (1829, p. 16, trans.): "the assemblage of individuals descended from one another or from common parents, and of those who resemble them as much as they resemble each other." *We see that the "New Systematics" is already rather old!* Therefore, it is a mistake to speak of a "revolutionary modification of the species concept" (Mayr, 1949, p. 102). Meglitsch emphasizes the same idea (1954, p. 52): "The classical systematist developed a system of classification upon the phenotypic, and especially upon the morphological, attributes, but while so doing they comprehended the species as an assemblage which is linked together genetically in some way or other The modern systematist, therefore, has not introduced a radically new element into the philosophy of systematics." Even Hennig (1950, p. 149, trans.) admits "that there has never been, up to the present time, a systematics in which typological and genetic principles were not connected together in the most intimate manner."

When I ask "What is a biological species?" I am asking for the general characteristics that differentiate the species of organisms from the species of inorganic nature (the elements, for instance). But the systematist is primarily interested in knowing what particularly applies to every species; he is asking for specificity which separates the individual species from each other. And this question can only be made to nature herself, and in no

case in which methodical observation is joined to intellectual penetration will a definite answer fail to appear. There are no taxonomic riddles relative to species limits, if these two conditions are fulfilled.

In modern literature there is much talk about "population systematics," but it is admitted that it is difficult to define the concept "population" adequately. Mayr (1949, p. 24) takes recourse to Webster's Dictionary! Homogeneous populations are at the disposal of every myrmecologist in any ant's nest. They facilitate knowledge of polymorphism, that is, of the phenotypical complex which belongs to *one* species. But it is a childish illusion to think that ants are "a group in which specific characteristics are so clearly and easily discernible," "because the myrmecologist is blessed with material which advertises its own specific characters" (Creighton, 1950, p. 12). "Population" is a taxonomically empty concept and has no meaning so long as the species to which it belongs is unknown. But the species can only be recognized by morphological comparison of several species of the same group and this comparison is always made on the individual. The individual is the "primary object of research" of the taxonomist (Remane, 1952, p. 3). Even in the examination of series, it cannot be "eliminated" as Rensch (1934, p. 15) asked, for it is self-evident that every series is composed of individuals. Also in plant taxonomy some authors are beginning to speak of "dynamic populations" and to scorn the herbarium. Rollins (1953, p. 183) laments this "tendency to deprecate specimens" and points to the fact that also the study of variation is based on individuals.

There are also numerous cases in which a single specimen shows such characteristic features that a description of it signifies a real advance in systematic research and an enrichment of the system. Some years ago, Reichensperger (1924) described a new ecitophilous genus and species in the family Histeridae, *Synetister pilosus*, from one specimen; the spe-

cies was found again 24 years later but was already sufficiently well characterized in the original description. In 1948 Brown described a minute ant from New Caledonia, *Discothyrea remingtoni*, from one holotype; as shown by the accompanying illustration, the species is so characteristic that recognizing it again should present no difficulty at all. In the Ecitonini also, various species are known only from single specimens, for example, *Labidus auropubens*, *Neivamyrmex inca*, *N. maxillosus*, *N. physognathus*, *N. cratensis*, *N. carinifrons*, *N. pulchellus*, *N. imbellis*, *N. planidens*, *N. cloosae*. I am convinced that all these forms can be immediately recognized from my descriptions and figures and that suppressing them or not describing them would have resulted in a perceptible gap in our knowledge of army ants.

The so-called "population systematist," as is well known, uses exclusively the genetic species concept and lays considerable emphasis on interbreeding and reproductive isolation. "This criterion has nothing to do with pure systematics" (Schindewolf, 1950, p. 442, trans.). The same origin and reproduction is a theoretical postulate, but not a general criterion for determination of species. Experiments of hybridization are possible only in rare cases and even the population systematist does not proceed without comparative morphology, as Mayr himself must admit (1949, p. 121). Morphological comparison is and will remain the backbone of any taxonomic research.

Geographic factors are also to be rejected as primary criteria in species systematics. Whether two species are "sympatric" or "allopatric" is completely immaterial to their differentiation. The question may be important to the theoretician on evolution, but it has only secondary interest for the systematist. "The system can only be based on what the organisms themselves are and on the characters they show. It must put us in a position to recognize and to name the forms even without knowledge of their

origin and distribution in space. We must first be able to determine the organisms, before we can establish their geographic distribution" (Schindewolf, 1950, p. 463, trans.).

It has been asserted that in difficult genera the comparative morphological method is not sufficient for segregation of the species. The botanist Rollins, Director of the Gray Herbarium at Harvard University, takes a position on this question in a very readable paper re-printed in "Systematic Zoology" (1953, pp. 180-190). He proceeds from the fact that in every genus there are species which can be readily separated. "I do not know of a single genus in which such species may not be found." Exact study of these species teaches that all of them differ by a majority of characters. "*Unus character, character nullus.*" The characters recognized as valuable form the "species standard," which is "the real key to species interpretation in the whole genus," including the more difficult series. In the genus *Arabis*, Rollins obtained reliable results by this method and he added: "I believe that the method would even permit agreement as to the number of species in *Rubus* or *Crategus*." This method is nothing other than the comparative morphological method mentioned above. It is consciously or unconsciously used by every monographer who goes thoroughly into the matter and is not satisfied with compilations. Of course, these ideas "are fairly radical deviations from the most common present-day ideas" (Rollins).

How many species shall be described? I answer: just as many as are present in nature, no more and no less. Ornithologists frequently speak of "simplification of the system" by reducing the number of species. If species which are not species are thereby eliminated, this tendency can only be welcomed. History teaches that there was no lack of such "species" in ornithology. But if some authors go so far to ridicule the description of really new species and to demand revisions or monographs in groups where is not yet the

slightest possibility for revisionary work, then they hinder the freedom of research and forget that the principal task of a systematist is to make the species of nature known. It is therefore difficult to understand why Horn (1929c, p. 59, trans.) presented the curious opinion: "It should be clear to the systematist that the greatest possible limitation of numbers of species is a most urgent prerequisite if we few entomologists are not to lose every future orientation." I ask: where then shall the boundaries be drawn? In his monograph on the South American weevil genus *Conotrachelus*, Fiedler (1940) lists 547 species, of which 404 are described as new. Marshall, a specialist in this group, estimates that the total number of species in this genus is probably 2000! In my opinion it would be nonsense to impose on the taxonomist any limitations other than those which are imposed by nature herself. It is a matter of course that modern standards must be applied in the case of new descriptions. Scientific systematics is more than a nomenclatural affair.

Schindewolf (1950, p. 433, trans.) speaks ironically of "purely naive descriptions of single species which, without any arrangement in a larger framework, provide only rough building stones. They represent a relapse into an epoch of research that has past." I consider this exaggerated. Every description of a species demands arrangement in a system and building stones are always building stones. Schindewolf also immediately withdraws his decision in that he adds: "With that, of course, no adverse judgment shall be passed at all on pure observation and exact description. They are *indispensable* and so far as they are carefully carried out they have lasting value and greater permanence than all the glittering hypotheses which are built on them."

The problem of species formation does not belong to systematics. Taxonomy is no "ancestor-hunting" (Blackwelder), but determination and classification of the products of evolution, i.e., of the species.

And this task is so difficult that it may be doubted if we will ever get to the end of it. Mayr's book, *Systematics and the Origin of Species* therefore, is already a failure in its title.

*The Subspecies (Race) as a Partial
Subcategory of the Species*

It has been known for a long time that certain species split into subspecies or races. Linnaeus and Fabricius commonly speak of "varieties." Kant (1775) was the first who recognized the difference between species, subspecies, and variety. Esper (1781, *De Varietatibus*) clearly defined: "Subspecies which are generally called varieties, are to be clearly separated from them. That they took their origin from species, is clearly revealed by the perfect similarity of the essential parts."

The subspecies was first introduced into zoological nomenclature by the ornithologist H. Schlegel (1844) who added a third Latin name to the name of the species (trinary nomenclature). This practice was taken up later by entomologists and is sanctioned today by the International Rules of Nomenclature. With Darwin's *Origin of Species* (1859) began a movement which can be designated as devaluation of the species. Through the fusion of the doctrine of *Formenkreis* (Kleinschmidt) and *Rassenkreis* (Rensch) with the evolution theory the cult of races came into full swing. Originally destined to cleanse the "Augean stable" (Kleinschmidt) of ornithological nomenclature, it was eagerly seized upon by the neodarwinists (Huxley, Rensch, Mayr) and proclaimed as "one of the most productive working hypotheses of taxonomy" (Mayr). All this led to an inflation of infraspecific nomenclature, which is a symptom of decline and deterioration of present-day systematics. Taxonomy is being reduced to an affair of nomenclature. Systematics becomes the science which gives a great many names to the same thing. According to Burt (1954, p. 99) 150 subspecies have been described

for *Thomomys bottae* alone, and there are more to come! Wilson and Brown (1953, p. 102) characterize the situation with the following remark: "From our experience in the literature we are convinced that the subspecies concept is the most critical and disorderly area of modern systematic theory."

Because of the abuse of "subspecies" in zoological nomenclature some authors "wish to abolish trinomialism root and branch" (Huxley). With that, there would be an end to "the tyranny of subspecific names." Such a panacea might be considered a successful solution in the case of many so-called "races" mentioned in the literature, for instance, those of *Passer domesticus* and *Phasianus colchicus* in Kleinschmidt (1926), or those of *Cyclophorus perdix* in Rensch (1934), or those of *Mimeogralla albimana* in Hennig (1950, p. 136). But things are not so simple if we look a little deeper into the matter and consult nature, instead of literature. "Study nature, not books," Agassiz used to say.

If we want to find out whether actual "subspecies" do exist in nature, we must proceed from the species. Only in well worked genera whose species are sufficiently known can the study of infraspecific variation be undertaken with any prospect of success. Now experience teaches that some species have a tendency to form races, others not. "The multiplicity of races of natural as well as of cultivated species is extraordinarily different. Without perceptible reason, we see that some species break up into a vast number of hereditary races (for instance, *Daphnia longispina*), while closely related species (*Daphnia pulex*) do not" (Woltereck, 1931, p. 290). The same observation can be made in ants. We find monotypic species together with polytypic ones, sometimes in the same genus. *Eciton hamatum* is constant, *E. vagans* and *burckhelli* split up into races. Wheeler (1936, p. 176) writes of *Termitopone commutata*: "The stability of the ant is attested by the fact that, so far as known, it exhibits neither

subspecies nor varieties in any part of its range." In his revision of the Dacetini, Brown found no races at all. With regard to the Diptera, Rensch (1947, p. 51, trans.), remarks: "It is striking that in this Order of insects geographic variation has hitherto been observed only sporadically." In phorid flies I never saw any race; even such wide-spread species as *Diploneura cornuta* and *Megaselia scalaris* are absolutely constant throughout their range.

Since all infraspecific variation is bound by the species limits, it is absurd to conclude that the polytypic species represents a special "collective category," in addition to the monotypic species. The Linnean species has not perhaps been "broadened" to include both kinds; it has embraced the non-dimensional and the multi-dimensional species from the beginning. The monomorphic species characters are constant in both. That a "tremendous clarification of the system" has been obtained by the distinction between monotypic and polytypic species, as Mayr, Linsley, and Usinger say (1935, p. 26), is an empty assertion. It could be said on the contrary, that the true species concept was destroyed, and the basis of all systematics was undermined. This danger was clearly seen by the botanist Wettstein who remarks "that the *Rassenkreis* of Rensch which goes beyond the species and means the establishment of a further systematic category beside the species, is a formal impossibility. General acceptance of this concept would bring chaos into systematics and would cause its collapse" (in Hennig, 1950, p. 83). Rothschild and Jordan (1906) called the *Formenkreis* "a kind of half-caste between species and subgenus." Plate writes (1914, p. 134, trans.): "The concept *Formenkreis* is superfluous if taken in the strict sense of the word, for it designates only the sum-total of all geographic variants of the species."

The basic fault of the *Formenkreis*-theory is the fact that it does not proceed from the species. Kleinschmidt writes (1926, p. 28, trans.): "The designation

'species' is ambiguous. . . . Therefore we cannot take the definition of the species as a starting point. . . . The species is a fiction of the human mind, by which a number of similar individuals are grouped together. The *Formenkreis* [form-cycle], on the contrary, is a natural unit. . . ." Some pages later (p. 33) Kleinschmidt seems to have forgotten that the species is "a fiction of the human mind," for then he declares the *Formenkreis* to be identical with the species of systematics. It should be clear that no "doctrine" can be erected on such feeble logic. The species is and remains the fundamental unit of the system, from which all research of infraspecific variation must begin.

Goldschmidt's investigations on *Lymantria* (1934) have proved that the *Rassenkreise* do not merge into each other and that races are not incipient species. In the Ecitonini I have reached the same conclusion. All the races of *Eciton burchelli*, for instance, remain strictly within the specific limits of *burchelli*, as do also the races of *vagans*, etc. There is no intergradation of any kind between races of different species, and in no case it is doubtful to which species a given race belongs. I conclude from that:

Race and species are not equivalent categories. Species are essentially different. Races are essentially alike, because they agree in all basic structures and are linked together genetically; they differ only gradually by accidental characters or slight hereditary modifications of basic characters. The race depends upon a splitting up of the species, it represents an "epiphenomenon" of the species (Kuhn). Therefore it is nonsense to ask whether an individual "still" represents a race or "already" represents a species. There is no living or fossil animal which does not belong to a given species. The species is primary, the race secondary. Every race shows the "facies" of the species from which it has been split off. By "facies of the species" I mean the complex of specific characters which are common to all races of the same species. This "facies" is always recognizable if the species of the genus concerned are accurately compared, in which comparison, of course, all the castes must be considered. All true species, though in some cases at first glance extremely similar, prove to be sharply separated by a bridge-

less gap, provided we do not proceed from one individual but rather take the whole complex of phenotypic characters into consideration. [Borgmeier, 1955, in translation.]

Both Rensch and Mayr admit that there are no transitions between different species or *Rassenkreise*. The contradiction lying in the fact that nevertheless "border-line cases between race and species" are constantly being mentioned, is so much the more remarkable. At most, border-line cases between races of the same species could be mentioned. Since the races of one species form a reproductive community, intergradations are able to occur. The races of *Eciton* that I investigated, both the allopatric and the partially sympatric ones, could be easily separated morphologically for the most part. Rensch (1947, p. 53, trans.) speaks of the "appearance of countless intermediate stages in each grade between races and species, and between weakly and sharply differentiated species." These alleged intergradations are a plain invention to rescue an idea, namely the idea of formation of species from races.

In my opinion it is wrong to say: "There is therefore no primary morphological difference between races and species, that is, the geographic races can be considered different far-advanced preliminary stages of the species" (Rensch, 1929, trans.). Here "race" is again being taken as an independent category, while each race clearly belongs to a definite species and all the members of a *Rassenkreis* distinctly differ specifically from those of any other. That morphological criteria are used both in separation of species and in discrimination of races, does not prove that the two categories are equivalent. Morphological characters are also used in the definition of genera, but no one claims that there is no difference between genus and species. Both species and race are universal concepts applied to biological units, but the racial characters already presuppose the specific characters and are, as it were, superimposed on them. Consequently there is indeed a *primary difference* be-

tween species characters and race characters, and the fact that the specific characters are retained in every formation of a race is clear evidence for the formation of races from species, but not of species from races. "Race-formation . . . [proceeds] from above downwards, but not, as the traditional theory of descent wants to have it, from below upwards . . ." (Conrad-Martius, 1949, p. 252, trans.). "Subspecies are actually, therefore, neither incipient species nor models for the origin of species. They are more or less diversified blind alleys within the species" (Goldschmidt, 1940). Schindewolf remarks on this (1950, p. 407, trans.): "From my personal experience I can only add that Goldschmidt's deductions completely satisfy the requirements that the fossil material seems to me to impose and that he is the first geneticist to present a comprehensive explanation which does justice to the real-historical, phylogenetical findings." Arcangeli, an Italian expert on Crustacea, writes (1951, p. 77, trans.): "The opinion has been expressed by many biologists that the subspecies into which a species can be eventually divided may represent new species in process of formation. . . . Truly this is an admission which, however suggestive it may be, is not supported by any evidence. On the contrary, it is a fact that in some cases there are circumstances that are opposed to precisely the same admission." In order to illustrate the "fixity of subspecies," Arcangeli cites cases from the genus *Tylos* Latr.

Conrad-Martius points out another contradiction in the *Rassenkreis*-theory to which generally no attention is paid.

While on the one hand they try to demonstrate the impossibility of separating species and races definitely and basically by the fact that frequently closely related species are much more similar to each other than the different races of one and the same species; on the other hand, the origin of the species *out of* the race is explained by the fact that the races must have removed themselves far enough from each other in their characters. According to this, different species would be expected to be separated by a sharper gap

than the races of one and the same species [1949, p. 258, trans.].

In all attempts to define the nature of the subspecies, geographic replacement plays a great role. Rensch (1934, p. 14) speaks of the "primacy of geographic distribution," but if we examine his statements more closely it will be seen that he is continuously working with morphological comparison. We find the same contradiction in Schilder (1952, p. 11), who wants to put "the mostly more precise criterion of distribution in space and time in the place of uncertain morphological differentiation." In spite of this affirmation, Schilder, too, always works with morphological methods. This contradiction between theory and practice is one of the best proofs of the primacy of form and the fundamental significance of morphology. No systematics can be erected on locality labels. Systematic research is unthinkable without comparative morphology.

From my experience with *Eciton* I am convinced that the subspecies can be purely morphologically conceived. But its recognition is more difficult than that of the species, because the differences are usually finer. The method for recognition of subspecies is about the same as that recommended by Rollins for the study of species. After the determination of the species we proceed from cases in which the racial differences are clearly evident, for instance, in the case of *Eciton vagans* from the subspecies *angustatum* and *mutatum* of which all castes are known. These then form the "standard" for recognition of the other races of the same species. Lack of material of sexual forms from the whole range of distribution often renders the results uncertain. Systematics is a science that grows by trial and error. Also exact determination of the nominal race is important. But most important is the comparative evaluation of the *individual* phenotypic characters which is the basis of systematic research. Such racial characters may be different in subspecies of the same species: propor-

tion of body parts, pubescence, coloring, etc.; nature does not follow a rigid scheme. In any case, only characters which are relatively constant and discontinuous come into question for separation of races. Bogert (1954, p. 112) very rightly says: "Subspecies should be recognized only when sharp discontinuities in the trends of one or more individual characters can be demonstrated." And Ferris remarks (1928, p. 57): "These forms should not be named if the characters upon which they rest are not perpetuated from generation to generation." Individual variation and grading variation (Huxley's cline) are taxonomically worthless and do not deserve denomination.

The geographic distribution of a given race can be determined only after the establishment of the morphological difference. As is to be expected, every race inhabits a partial zone of the total area of distribution of the species. In contrast to species, the subspecies is geographically definable, but geographic isolation is rather a condition of morphological differentiation, not its cause. Subspecies can originate abruptly by mutation in any place within the range of the species. The primary factors of race-formation seem to be endogenous; exogenous factors have at most an auxiliary function. The race, therefore, is not a type of adaptation to the landscape as is frequently asserted. No racial character of *Eciton* has any adaptive significance.

According to Mayr the subspecies is a purely subjective concept. According to Brown and Wilson it is a "typological relic," and they add (1954, p. 176): "The experience of the past year has strengthened our opinion that any particular subspecies pattern is determined arbitrarily by the individual taxonomist's choice of characters, and any trinomen employed is fitted uncomfortably to a minority of the geographic variable characters." It must be admitted that many "subspecies" (perhaps most of those mentioned in the literature) are "authors' subspecies." It may even be that I have myself erred in the

evaluation of subspecific characters in some cases in *Eciton*. But I am firmly convinced that there are true subspecies in nature, that the subspecies is justified as a partial subcategory of the species, that it is a biological unit existing as an objective reality independent of man's contemplation which forms the basis for the concept "subspecies" (or "race"). I am further convinced that careful morphological comparison will lead to certain recognition of such concrete entities and that, for example, no competent taxonomist will succeed in demonstrating that *angustum* and *mutatum* are not valid subspecies of *Eciton vagans*. The distinctive characters were not selected arbitrarily, they were derived from nature. To call the two forms "species" would be quite illogical, as long as comparative morphology is considered as the basis of systematic research.

In summary, I am defining the subspecies or race as a relatively constant, discontinuous variant of the species. Since not all species form races, this is not a universal category of fundamental significance, but rather a partial subcategory of species. The systematist should by no means neglect the study of subspecies, nor should he regard it his primary task. The first aim of all taxonomic research is the determination and definition of species as the fundamental units of the system.

Conclusion

I am convinced, with Blackwelder and Boyden, that the introduction of evolutionary concepts into systematics has produced great confusion. The systematist may not be anti-evolutionary, but in practice he is non-evolutionary.

No matter how convinced an evolutionist may be in theory, no naturalist and, more specially, no biologist, can work and think in that way. The systematic zoologist may assert that he is a thorough-going evolutionist, but as soon as he sits down at his table to work with his specimens, he begins at once to sort things into categories, to define and limit, and, as he does so, is perfectly satisfied that he is in contact with reality and that the method he

adopts, suffices to make reality known. In other words, although he may do his best to believe in his evolutionary metaphysics, he cannot live it. He cannot think without logic nor define without concepts; and if he is to retain any belief in his work and in the validity of his science he must, in point of fact, proceed on the assumption that something corresponding to his concepts actually exist in Nature—that through them he attains a true knowledge of reality. To put the point in another way, he is forced in practice to admit that there is fixity in Nature, that a variety of different and distinct things actually exists. The zoologist may affirm, and sometimes does affirm, his complete disbelief in the reality of species, but it is in the definition of these alleged unrealities that he spends his working life [Thompson, 1937, p. 194].

Therefore, in opposition to Mayr's assertion (1949, p. 23) that 90 percent of modern taxonomic work consists in the study of variation, I venture to say that 100 percent of systematic research consists in the investigation of the stable elements in Nature. The principle task of the systematist is not "that of detecting evolution at work" (Huxley), but is the study of the work of evolution.

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